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Spatio-temporal variation in pre-dispersal reproductive losses of a Mediterranean shrub, *Euphorbia dendroides* L.

Abstract The factors that reduce the pre-dispersal reproductive potential of *Euphorbia dendroides* are identified and the magnitude and variability of their effects are examined, both on a spatial and on a temporal scale. The aims of the study were: (1) to assess whether such variation was related to plant attributes describing size and/or fecundity, and (2) to determine the consistency of those effects in plant reproductive success. Pre-dispersal losses were measured over 3 years in a total of 45 plants from two populations in Cabrera island (Balearic Islands, western Mediterranean). Two types of insect-plant interactions (a moth that preys on the inflorescences and a wasp that feeds on the seeds) significantly reduced the potential number of seeds of *E. dendroides*, whereas lack of ovary in the cyathium, ovary abortion or seed abortion were the causes of reproductive loss that can be considered "intrinsic" to the plant. Significant variation was found both spatially and temporally in their effects, though such variation could not be attributed to the plant traits measured. Moths and wasps were not found to exert any opposing selective pressure on the plant, and their effect was additive. Key factor analyses performed with the data obtained over three seasons showed that the influence of a factor on among-plant variation in total reproductive losses cannot be predicted by the magnitude of the loss caused by such a factor; thus, seed abortion, while representing a low reproductive loss (< 20% of the potential seed production) accounted for the greatest among-plant variation in total losses. The analyses also showed that the contribution of the plant-insect interactions to the variation in total losses varied significantly both spatially and temporally. This lack of consistency, together with the lack of association with the plant traits measured, suggests that the demographic changes produced by these interactions are unlikely to translate into adaptive changes.

Introduction

A large number of studies have quantified the effect of insects on pre-dispersal reproductive losses of their host plants (see, for instance, reviews in Crawley 1989, 1992), showing that large percentages of the potential seed crops of many species can be destroyed (e.g. Janzen 1971; Breedlove and Ehrlich 1972; De Steven 1981; Scott 1982; Auld 1986; Andersen 1989; Evans et al. 1989) with the possibility of limiting plant recruitment (Louda 1982a, b). Only a small proportion of these studies, however, have examined the consistency in the spatio-temporal variation of such effect. Moore (1978) found much consistency among individuals in seed attack by weevils in *Crotalaria* and attributed variation in seed crop losses among seasons to transient predator satiation. De Steven (1983) and Auld (1986) found the percentage of seed predation by weevils in *Hamamelis* and *Acacia*, respectively, to vary strongly with plant fecundity, also attributing some variation to predator satiation. Andersen (1989) showed strong differences in pre-dispersal seed losses to insects in *Leptospermum* between species, seasons, sites and individuals, and found that relative abundance of seed predator species contributed to spatial variation whereas fruit density contributed to temporal variation. Hails and Crawley (1991) observed much consistency through time in the striking differences in rate of insect-galling in oak, predicting that acorn crop was the key factor in causing population change among years. Much of the variation in all these studies,

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however, remains unexplained because the dynamics of the insect populations is largely unexplored.

Insects can act as selective forces by discriminating between phenotypes, resulting in individual variation in reproductive losses (Harper 1977). A particular plant trait may be selected due to the pressure exerted by an interaction (e.g. plant/pollinator, plant/herbivore, plant/disperser). To determine this, we need to know if and to what degree the demographic change produced by a given interaction translates into an adaptive change (Heithaus et al. 1982; Jordano 1989; Traveset 1994). Information on how consistent in time and space the effect of a particular interaction is in promoting variation in plant reproductive success will indicate the evolutionary importance of such an interaction for a plant population, and will give understanding of its overall effect on seed production. On the other hand, studying the variability in the risks of death will also help to identify the mechanisms of plant population dynamics, as variation in reproductive losses can promote the coexistence among plant species, enhancing plant diversity by preventing superior competitors excluding inferior ones (Crawley 1992).

The goals of the present study were to examine:

1. The magnitude of the reproductive losses caused by two species of insects (a moth and a wasp) that attack *Euphorbia dendroides* L. and of the losses due to factors other than insects (lack of ovary, ovary abortion, or seed abortion)
2. The variation within and between populations in such losses
3. How such variation relates to particular traits of the plant
4. Whether wasps and moths exert opposing or parallel selective pressures on the plant
5. The consistency of attack by the two insects on individual plants among years
6. The among-year variation in the relative contribution of each factor affecting the reproductive potential to the variation in total reproductive losses among individuals.

Information on the natural history of the plant and the insects is presented as this system has not previously been studied.

Materials and methods

Study area

The study was performed on Cabrera island, south of Mallorca (Balearic Islands). Cabrera is ca. 1130 ha and has a maximum elevation of 172 m. The vegetation is mediterranean scrubland, dominated by *Pistacia lentiscus*, *Phillyrea* spp., *Olea europaea*, *Juniperus phoeniceae*, *Cistus* spp., *Rosmarinus officinalis* and *Erica multiflora*. In some parts of the island, mainly in the northeast, *Pinus halepensis* is dominant. *Euphorbia dendroides* grows abundantly all around the harbour area and in Cala Gandulf, although it can also be found in other parts of the island.

Mean monthly temperature ranges from 8 °C (January) to 34 °C (August). Total annual precipitation is low, rarely exceeding 500 mm; in 1993 it was 489.1 mm (this figure is not available for 1992). The average for the period 1950–1971, obtained at the closest station south of Mallorca island, was 380 mm, ranging from 193 to 555 mm. A detailed description of the climate of Cabrera Archipelago and its vegetation can be found in Alcover et al. (1993).

Study organisms

Euphorbia dendroides L. (Euphorbiaceae) is a shrub, usually single-stemmed, that can reach 2 m in height and nearly 2 m in width. It is common in the litoral thermophilous scrubland of the central Mediterranean region, the Balearic Islands (excluding the Pithyusic islands), the Tirrenic islands and the ligur-provenzal coast, reaching some coastal localities of northeast Catalonia (Bolós 1958). The flowering period is usually in March, although in some years it can begin as early as mid-February and last until mid-April. Each adult plant produces hundreds to thousands of inflorescences (cyathia) grouped into clusters (cymes) of one to five cyathia. Usually each cyathium consists of a single female flower with a three-lobed ovary and several male flowers, surrounded by four to five round orange-coloured glands which produce copious, viscous nectar. This nectar is usually collected by flies of the *Calliphora* genus, although wasps and bees also act as pollinators of this plant (A. Traveset, personal observation). Preliminary observations suggest that there might be some pollen limitation due to the low frequency of insects visiting the inflorescences. The endemic lizard, *Podarcis lilfordi* (Günther) (Lacertidae), has been observed climbing the shrubs, lapping the succulent nectar and getting its snout covered by pollen, which suggests that this animal may also act as a pollinator of the plant. Small ants of the species *Plagiolepis pygmaea* (Latr.) are occasionally observed on the nectaries, although they probably act as nectar robbers.

The fruits reach full size several weeks after fertilization, and mature usually between the end of April and mid-May. They consist of a three-lobed green capsule that explodes when dry, catapulting the three small brown seeds away from the plant. Each seed (2–3 mm long) bears a whitish elaiosome which, in Cabrera island, is eaten by ants of the genus *Aphaenogaster*. These ants carry the seeds to their nests, thus promoting a secondary seed dispersal (A. Traveset, personal observation).

The adult of the microlepidopteran *Acrolita subsequana* (Herrich-Schäffer, 1851) (Tortricidae), a polyvoltine species specific to the genus *Euphorbia*, oviposits inside the buds very early in flower development. Small larvae (ca. 2 mm) can be observed within a cyathia before it has opened. As larvae grow, they join the adjacent cyathia together with the surrounding leaves, usually damaging the whole cluster of cyathia and precluding the development of ovaries. If the ovaries were already developed before attack, they usually abort at an early stage or produce capsules with aborted seeds inside. Only occasionally is there more than one larva per cluster. The larvae develop for several weeks until reaching the pupal stage, which takes place in the soil. Adult emergence occurs about a month later. So far, it is unknown whether this moth has other hosts in which it can develop. Its major predator during the larval stage is a wasp, *Ancistrocerus ebusianus* (Eumenidae), which is frequently observed on the flowering plants searching for larvae in the damaged clusters. These damaged clusters (both leaves and cyathia) soon dry up and are easily distinguished from the intact ones.

The wasp that attacks the seeds of *Euphorbia dendroides* belongs to the genus *Bruchophagus* (Eurytomidae). Adults can be observed ovipositing on the full-sized fruits by mid-April. Only one adult emerges per seed which indicates that each seed can bear only a single larva. The insect remains inside the seed at the larval stage through the winter and the adult emerges the following spring, when fruits are again available for oviposition. The wasp is thus a univoltine species and appears to be host-specific. The main predator of this species is a hemipteran, *Brachypelta aterrima* Forst

(Pentatomidae). which is commonly seen on the fruits puncturing the seeds in search of the larvae.

Inflorescence infestation by the moth

In the spring of 1992, a total of 15 individuals of *E. dendroides* were haphazardly chosen from a population (S'Espalmador, ES hereafter) on Cabrera island. During the flowering period. I recorded the total number of cyathia produced and those infested by moth larvae in all individual plants. The following year, I again recorded the number of cyathia infested by moths in those 15 individuals examined in 1992 plus in 3 additional plants in the ES population. In order to determine whether moths discriminate among cymes (clusters) bearing different number of cyathia. I recorded the number of total cyathia contained in the infested and in the uninfested cymes.

In spring of 1994, cyathia infestation was examined in 29 individuals (which included those examined in 1992 and 1993) from ES and in 15 from Cala Ganduff (CG hereafter). a different population ca. 2 km from ES. In the previous 2 years, cyathia infestation in the CG population was negligible and was not recorded.

For each individual plant, I measured three attributes indicative of plant size: height. maximum crown diameter. and diameter at 10 cm from the trunk base.

Seed infestation by the wasp

On 21 May 1992. I collected fruits from 45 individuals, haphazardly chosen from the two populations: 30 from ES (including those in which I examined moth infestation) and 15 from CG. After having measured the total crop per plant (total number of fruits produced), I collected between 30 to 50 maturing fruits from each, placing them in paper bags. These fruits came from intact cyathia, i.e., those which had not been infested by the moth. Once in the laboratory, I dissected a total of 50 seeds per plant which were randomly chosen after breaking apart each fruit (a capsule contains 3 seeds). For each dissection I recorded whether the seed (1) contained a larva. (2) was aborted (empty) or (3) contained a viable embryo surrounded by white endosperm which filled the seed locule.

In the spring of 1993 (11–12 May) and 1994 (29 April), I again counted the number of fruits produced by the same plants examined in 1992 in the two populations and collected fruits to evaluate the proportions of viable, aborted or wasp-damaged seeds. I also dissected 50 seeds (when available) per plant, which were randomly chosen from the collected capsules.

Data analysis

The SAS statistical package (SAS 1987) was employed to perform all correlations, regressions. and analyses of variance. A key factor analysis (Podoler and Rogers 1975) was used to estimate the rela-

tive contribution of factors that influence plant reproductive potential to variation in total pre-dispersal losses among individuals. In this analysis. the estimated reproductive loss at each phase is regressed against the total loss of reproductive structures. and the slopes of the regressions are used to determine the relative influence that each factor has on among-plant variation in total pre-dispersal losses [see Heithaus et al. (1982) and Jordano (1989) for similar analyses]. This analysis was used for the data obtained from ES over the 3-year period and for those obtained from CG in 1994.

All means are accompanied by their standard deviations throughout the paper unless otherwise indicated.

Results

Plant fecundity

The total number of cyathia, the proportion of cyathia that gave fruit and the total fruit crop recorded per plant over the 3 years are shown in Table 1. There was much variation in each of these variables, being lower for the number of cyathia than for the number of fruits (Table 1). Number of cyathia was always correlated with plant size (Table 2), although in 1992 the correlation was significant only with plant height, not with crown or trunk diameter. Cyathia production did not vary significantly among the 3 years in the ES population ($F_{2,47} = 2.43$, $P > 0.05$) (total number of cyathia in CG was recorded only in 1994).

Fruit production in 1994 was significantly associated with all attributes indicative of plant size as well as with number of cyathia produced. but this was not the case for the previous 2 years (Table 2). This lack of correlation is probably due to the spatially and temporally variable number of cyathia that do not produce any fruit either because they lack ovaries or because they are infested by moths (see next section).

The proportion of cyathia giving fruit (fruit set) was always negatively correlated with the proportion of cyathia infested. although in the 1st year the correlation was not significant ($r_s = -0.37$, $P > 0.05$; $r_s = -0.68$. $P < 0.01$, and $r_s = -0.89$, $P = 0.0001$. for 1992, 1993 and 1994, respectively). Fruit set was not consistently associated with plant size: in 1992 the correlation was not significant. and in 1993 larger plants had a lower fruit set whereas in 1994 the opposite was found (Table 2).

Plants in the CG population were significantly taller than those in ES (132.6 ± 25.3 versus 83.4 ± 26.6 cm,

Table 1 Plant fecundity and infestation of cyathia by moths in the two plant populations (*ES* S'Espalmador, *CG* Cala Ganduff) studied from 1992 to 1994. Means and standard deviations are given. The number of plants, *n*, is given in parentheses

Area	Variable	1992	1993	1994
ES	No. of cyathia	319.4 ± 149.8 (15)	553.1 ± 389.5 (18)	584.5 ± 390.3 (29)
	% Fruit set	34.5 ± 27.0 (15)	28.9 ± 29.1 (18)	23.8 ± 18.7 (29)
	% Cyathia infested	39.1 ± 26.9 (15)	65.8 ± 22.7 (18)	73.6 ± 25.2 (29)
	No. of fruits	141.9 ± 133.6 (29)	148.6 ± 134.5 (28)	142.9 ± 128.5 (29)
CG	No. of cyathia	–	–	1246.7 ± 795.4 (15)
	% Fruit set	–	–	62.3 ± 10.7 (15)
	% Cyathia infested	–	–	0.8 ± 1.3 (15)
	No. of fruits	450.3 ± 992.2 (15)	589.3 ± 643.9 (15)	870.1 ± 735.5 (15)

Table 2 Correlations between traits indicative of plant size (*ht* height, *cd* crown diameter, *td* trunk diameter) and fecundity (*nc* number of cyathia, *nf* number of fruits, *fs* fruit set) during the 3 years of the study. Data from the two populations are pooled

	ht	cd	td	nc	nf	fs
ht	–	0.71***	0.71***	0.61*	0.31	0.26
				0.63**	−0.14	−0.64
				0.56***	0.55***	0.45**
cd		–	0.73***	0.50*	0.45**	0.18
				0.57**	0.04	−0.49*
				0.74***	0.72***	0.30*
td			–	0.51*	0.26	0.14
				0.53*	0.11	−0.20
nc				0.79***	0.79***	0.35*
				–	0.45	0.15
					0.23	−0.17
					0.93***	0.37**
nf					–	0.86***
						0.78***
						0.84***
fs						–

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.0001$

Fig. 1 Relationship between number of cyathia produced and number of cyathia infested by the moth *Acrolita subsequana* in 1992 (*open squares*; $r = 0.59$, $P = 0.02$, $n = 15$) and in 1993 (*solid dots*; $r = 0.91$, $P = 0.0001$, $n = 18$)
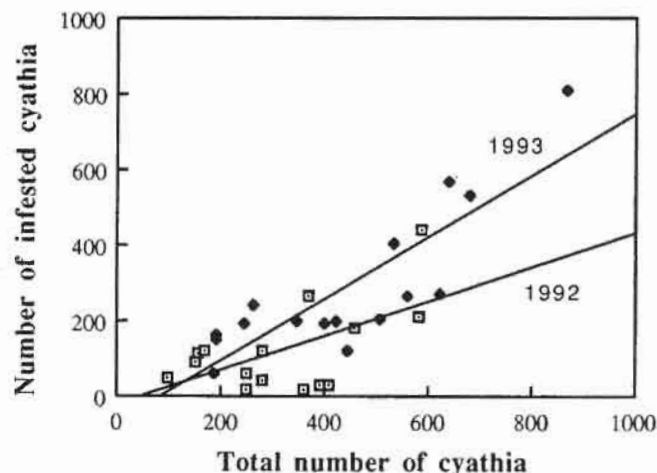
respectively; $F_{1,42} = 35.12$, $P = 0.0001$), had a wider crown (131.5 ± 40.3 versus 102.7 ± 28.7 cm; $F_{1,42} = 7.52$, $P = 0.01$) and a wider trunk (4.8 ± 2.5 versus 3.6 ± 1.3 cm; $F_{1,42} = 4.57$, $P = 0.04$) and produced consistently more fruits than plants in the ES population during the 3 years of the study (Table 1). A repeated measures ANOVA showed that fruit production varied significantly between the two areas ($F_{1,41} = 11.78$, $P < 0.01$) and among years ($F_{2,82} = 9.94$, $P = 0.0001$). That differences in fruit production among years were not equal for the two areas (fruit production being greater in CG than in ES) was indicated by the significant interaction between the two factors ($F_{2,82} = 10.92$, $P = 0.0001$). The relationship between plant size and fruit crop did not differ significantly between areas ($P > 0.05$). This was determined by performing an analysis of covariance that showed homogeneity of slopes between the two populations.

There was a strong consistency among years in plant fecundity (all $r > 0.75$, $P = 0.0001$), i.e., the plants that produced the highest number of fruits in 1992 were also the most fecund in 1993 and in 1994.

Losses due to the moth

The number of cyathia that were infested in 1992 varied greatly among individuals, ranging from 17 to 440 (mean 119.5 ± 116.0, $n = 15$), and was correlated with the total number cyathia produced (Fig. 1). The proportion of cyathia that were infested was, on average, about 40% (Table 1) and was not associated with any of the plant attributes related to plant size ($P > 0.05$).

In 1993, the moth attacked an average of 376.8 ± 318.8 cyathia per plant (range 63–1126, $n = 18$), which

represented about 65% of the cyathia produced (Table 1). In contrast to 1992, the proportion of cyathia damaged was significantly associated with plant height, taller plants suffering relatively greater damage ($r_s = 0.61$, $P = 0.007$). As in 1992, the absolute number of cyathia damaged was significantly correlated with number of cyathia produced (Fig. 1), but the relative number was not ($r_s = 0.20$, $P > 0.05$). The number of cyathia per cyme, which ranges from 1 to 6, did not affect moth oviposition, i.e. the relative number of cyathia attacked did not differ significantly among cymes bearing different numbers of cyathia ($F_{4,75} = 0.21$, $P > 0.05$).

In 1994, the number of infested cyathia was 299.3 ± 368.2, ranging from 0 to 1400 ($n = 44$ plants). It was neither correlated with plant size nor with total number of cyathia. The proportion of cyathia damaged by the moth was significantly greater ($F_{1,42} = 123.5$, $P = 0.0001$) in ES than in CG (Table 1). The proportion of moth-damaged cyathia was not associated with plant size either, but it was associated with the total number of cyathia produced ($r_s = -0.32$, $P < 0.05$), more fecund plants having relatively lower damage.

Significant differences ($F_{2,47} = 10.9$, $P = 0.0001$) were found among years in the proportion of cyathia damaged by the moth (Table 1). However, individual trends were strongly consistent (all $r_s > 0.70$, $P < 0.01$), i.e. plants with the greatest damage in 1992 were also the most infested in 1993 and in 1994.

Losses due to the wasp

In 1992, a high proportion of seeds were killed by wasps (Table 3). There was much variation between plants in wasp predation, ranging from 37 to 93% ($n = 45$). In the following years, the incidence of wasps in the seeds

Table 3 Percentages (mean and standard deviation) of seeds that are (1) preyed on by wasps, (2) empty (aborted), or (3) viable (with an embryo and endosperm filling the seed locule) in the two plant populations (*ES* S'Espalmador, *CG* Cala Gandulf) during the 3 years of the study. The number of plants is given in parentheses

Area	Variable	1992	1993	1994
ES	% Seed predation	67.7 ± 13.7 (30)	22.5 ± 21.8 (26)	44.4 ± 20.8 (27)
	% Seed abortion	22.6 ± 15.2 (30)	37.7 ± 30.1 (26)	32.1 ± 26.6 (27)
	% Seed viability	9.8 ± 7.9 (30)	39.8 ± 24.8 (26)	23.4 ± 14.5 (27)
CG	% Seed predation	78.4 ± 9.1 (15)	37.5 ± 26.3 (15)	24.7 ± 14.1 (15)
	% Seed abortion	14.4 ± 7.6 (15)	28.9 ± 32.6 (15)	28.7 ± 20.5 (15)
	% Seed viability	7.1 ± 7.6 (15)	33.6 ± 18.6 (15)	46.7 ± 23.1 (15)

of the same plants was lower (Table 3), ranging from 0 to 78% in 1993 and from 0 to 74% in 1994. A repeated measures ANOVA showed that seed predation rates did not differ significantly among areas ($F_{1,37} = 0.25$, $P > 0.05$) but did differ over time ($F_{2,74} = 79.8$, $P = 0.0001$) and there was no significant interaction between these two effects ($F_{2,74} = 11.72$, $P = 0.0001$). No individual consistency in susceptibility to seed predation by wasps was observed, and none of the attributes related to plant size or fecundity were found to influence such predation (all $P > 0.05$).

There was no significant correlation between reproductive losses due to the moth and those due to the wasps in any of the 3 years (all $P > 0.05$): thus, plants with a pronounced moth infestation may or may not suffer pronounced seed predation by wasps.

Seed abortion

A relatively high proportion of the seeds produced appeared to be empty, with no embryo and with a seed coat that was soft and whitish. The proportion of abortions was 20% in 1992 (range 0–60%, $n = 45$ plants), 34% in 1993 (range 0–100%, $n = 41$ plants), and 31% in 1994 (range 0–95%, $n = 42$ plants). Seed abortion rates did not differ significantly between areas ($F_{1,37} = 0.89$, $P > 0.05$) but did differ among years ($F_{2,74} = 6.68$, $P = 0.002$) and no interaction between these two factors was observed ($F_{2,74} = 0.17$, $P > 0.05$) (Table 3).

Seed abortion was not associated with plant size or fecundity in any of the 3 years ($P > 0.05$). There was some consistency through time, since plants that showed the highest rate of abortion in 1994 were also those with the highest rate in 1992 and in 1993 ($r_s = 0.53$, $P < 0.01$ and $r_s = 0.48$, $P < 0.02$, respectively) although there was no significant correlation between abortion rates in 1992 and in 1993.

Production of viable seeds

Table 3 shows that the fraction of seeds that were viable (with full endosperm and embryo) was especially low in 1992, representing on average only 9% of the total number of seeds ($n = 45$). It was quite variable among plants, some individuals producing no viable seeds at all and others producing up to 30% of the seed crop. In 1993, seed viability was greater, averaging 37% and ranging from 0 to 98% ($n = 41$). In 1994, 32% of the seeds were viable ($n = 42$) on average, ranging from 0 to 86%.

No significant differences in the proportion of viable seeds were found between areas ($F_{1,37} = 1.29$, $P > 0.05$) but great differences were observed among years ($F_{2,74} = 30.06$, $P = 0.0001$) (Table 3). The differences among areas varied through time, as indicated by the significant interaction between these two effects ($F_{2,74} = 9.36$, $P = 0.0002$).

None of the plant attributes related to size or fecundity influenced the proportion of viable seeds produced in any given year, and consistency in seed viability was found only between the two last years ($r_s = 0.52$, $P = 0.008$).

Cumulative effect of the factors affecting reproductive potential during the pre-dispersal phase

Four factors were identified to affect the reproductive potential of *E. dendroides* during the pre-dispersal phase (Table 4). The relative ecological importance of losses at each stage was quantified as the proportion of the initial crop size lost during that stage. The potential number of viable seeds, estimated by multiplying the initial number of cyathia produced by three (each cyathia produces a single fruit containing three seeds) was greatly reduced in each of the 3 years of study to an average of: 32.0 ± 32.5 ($n = 15$) viable seeds per plant in 1992, representing a loss of 97%, 212.1 ± 211.6 in 1993 (a 87% reduction, $n = 18$), and 118.6 ± 115.5 (93% reduction, $n = 27$) and 1336.5 ± 1294.2 (64% reduction, $n = 15$) in ES and CG, respectively, in 1994 (Fig. 2).

In the ES population, damage of cyathia by the moth accounted for most of the losses in the 3 years, from 39% to 74% (Table 4; Fig. 2). The next most important cause of reproductive loss in 1992 and 1993 was the lack of ovary production or ovary abortion (27% and 10%, respectively), and in 1994 it was seed damage by wasps (13%). Seed predation by wasps represented between 6% (in 1993) and 20% (in 1992) of reproductive losses in the ES population, while seed abortion did not exceed 12% in any of the 3 years (Table 4).

Table 4 Factors that contribute to the losses in the reproductive potential of *Euphorbia dendroides* during the pre-dispersal phase and results of the key factor analysis. The key factor *slope* indicates the relative influence of each factor on variation in total losses (see text for its calculation) while *r* is the correlation between total losses and losses due to each factor. Data were log transformed before analyses. For 1994, data from S'Espalmador (*ES*) population (*top line*) and from the Cala Gandulf (*CG*) population (*bottom line*) are given. *x* is the mean proportion of the initial crop size lost due to each factor

	1992				1993				1994			
	x	CV	Slope	*r*	*x*	CV	Slope	*r*	*x*	CV	Slope	*r*
Infestation of cyathia by moths	0.39	68.8	0.078	0.20	0.66	34.8	0.14	0.26	0.74	33.8	0.66	0.51**
									0.008	159.4	0.01	0.73**
Lack of ovary/ ovary abortion	0.27	91.5	0.101	0.17	0.10	139.5	0.29	0.61**	0.07	180.1	−0.20	−0.23
									0.34	39.7	0.18	0.45
Seed damage by wasps	0.20	80.1	−0.008	−0.03	0.06	135.1	−0.03	−0.17	0.13	87.7	−0.12	−0.54
									0.17	71.8	0.16	0.51*
Seed abortion	0.12	112.4	0.829	0.76	0.09	112.1	0.59	0.83***	0.05	87.6	0.66	0.83***
									0.19	75.4	0.65	0.86***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Fig. 2 Reduction of the reproductive potential of *Euphorbia dendroides* through the pre-dispersal phases in the ES population during the 3 years of study and in the CG population in 1994. The following stages are represented in the *x* axis: *1* initial crop size (number of cyathia × 3 seeds/cyathia); *2* crop size after subtracting the cyathia infested by the moth; *3* number of seeds in the fruits produced (number of capsules × three seeds/capsule) (the difference between *2* and *3* is the loss due to lack of ovaries or to ovary abortion); *4* number of seeds after subtracting those damaged by wasps; *5* number of viable seeds (the loss between *4* and *5* is due to seed abortion). Standard error bars are shown
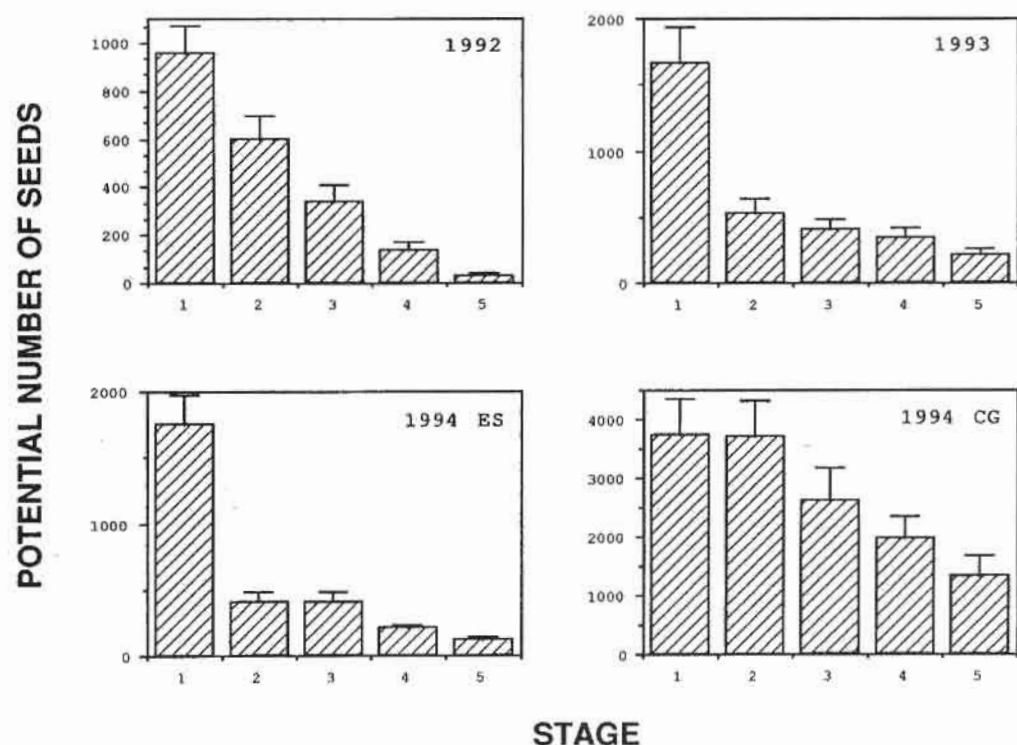
In the CG population, the main loss of fecundity in 1994 was due to lack of ovary production or ovary abortion (34%), followed by seed abortion (19%) and seed predation by wasps (17%). Loss of cyathia due to the moth were negligible (<1%) in all years. In 1992 and 1993, seed predation by wasps represented a much greater absolute fecundity loss than seed abortion (Table 3); the initial number of cyathia was not recorded in this area during either 1992 or 1993, so losses due to lack of ovaries/ovary abortion cannot be determined.

In ES, the variable that showed the highest among-plant variation in reproductive losses varied between years. In 1992, it was seed abortion (CV=112.4%),

while in 1993 and in 1994 it was lack of ovaries or ovary abortion (139.5% and 180.1%, respectively). In CG, loss of inflorescences due to moths showed the highest among-plant variation (159.4%) whereas lack of viable ovaries showed the lowest (39.7%). In contrast, damage by moths showed the lowest variation during the 3 years of the study in ES.

The key factor analysis showed that seed abortion had the steepest slope for the 3 years of the study, in both populations (Table 4), indicating that the greatest contribution to among-plant variation in total loss of reproductive potential is due to this factor, even though it accounts for a low reproductive loss

compared to the other factors. In 1994, however, and only in ES, losses due to moths also had a large contribution to among-plant variation in total losses while representing the main important loss (74% of the initial crop) (Table 4).

Discussion

Spatio-temporal variation in plant fecundity

Euphorbia dendroides showed great variation in fecundity, mainly at a spatial (inter-individual) scale. Such spatial variation in number of cyathia produced was largely attributed to differences in plant size: taller plants, with a wider crown and trunk diameter, generally produced a greater number of cyathia (although not always a greater number of fruits). The low values of fruit set observed are due to several factors: a large fraction of cyathia lack ovaries; another fraction aborts them, and another is infested by moths. In the CG population fruit set was greater than in ES, mainly due to the much lower moth infestation of the former population. All these particular reproductive losses result in an even greater variability in fruit production than in cyathia production. Thus, it appears that reduction in potential fertility increases fitness variation among individual shrubs. The reason why the correlation between fruit crop and cyathia crop varies among years is probably because it depends on the variability of those reproductive losses and on how such losses are related to plant size and/or fecundity. That fruit crop and cyathia crop were significantly correlated only in 1994, for instance, might be (at least in part) because in that year more fecund plants suffered relatively lower damage by moths; in the previous years, in contrast, the plants that produced the largest amount of cyathia were also those that bore most infested cyathia (Fig. 1).

Both pollen and resource limitation, together with bet-hedging and selective abortion are usually found to be the causes of low values of fruit set (e.g. Stephenson 1981; Bawa and Webb 1984; Sutherland 1986; Krusi and Debussche 1988; Charlesworth 1989; Ehrlén 1991). In the present system, the large proportion of cyathia lacking an ovary in some individuals might indicate a limitation of resources, whereas the low frequency of insect visits observed suggests that pollen might also be limiting the reproductive output of the plant.

A strong consistency in fecundity was found across years, so plants with the greatest fruit crops in 1992 were also the most productive in 1993 and in 1994. A rather low temporal variation was found in fecundity, possibly due to the similar weather conditions during the three flowering seasons. The average number of fruit produced in ES were quite similar across the 3 years (see Table 1); in CG, the temporal variation was greater, plants being more fecund in 1994 than the previous 2 years, which indicates that other variable factors

besides weather (e.g. insect abundance, nutrient limitation) are affecting plant fecundity.

Variation in pre-dispersal seed losses

The damage of cyathia by *Acrolita subsequana* represented an important reproductive loss in the ES population, reaching 100% in some individual plants. In contrast, the effect of moths was negligible in CG. The two populations are nearby (less than 2 km apart) and the surrounding vegetation is quite similar. The only apparent difference between the two areas is that ES is oriented to the northeast whereas CG is oriented to the northwest. Whether this difference is the main cause determining moth infestation is unknown. Another possible cause of the differences observed between both populations might be related to the presence of the wasp, *Ancistrocerus ebusianus*, that preys on the moth larvae; it is unknown, however, whether levels of larval predation by wasps differ between the two areas. It also remains unknown how far the adult moth travels to infest a new host; if it stays on the same host from which it emerged, this might contribute to the consistency of attack observed from year to year among individuals.

There was great variation among plants within a population in the levels of infestation. Such variation, however, could not be attributed to the traits measuring size or fecundity; the exception was in 1993, when taller plants tended to suffer greater damage. In other systems (e.g. De Steven 1981; Evans et al. 1989), moths have been found to reduce the reproductive potential by more than 80%, but predation intensity was not related to plant fecundity in these studies either. Evans et al. (1989) found that flowering time affected moth oviposition; in the system studied here, however, this factor is apparently irrelevant, as moths were observed from the beginning to the end of the flowering period, and the plants examined flowered synchronously. Differences in damage among plants might well be more related to differences in plant palatability (Thompson 1985), quality of foliage (Harrison 1987) or other forms of plant resistance (Green and Palmbald 1975) than to differences in timing or density of flower or fruit production (Janzen 1971; De Steven 1983; Auld 1986). The microhabitat where the plant is located (e.g. sun versus shade) also can influence plant preference in many herbivores (White 1984).

Temporal variation in cyathia infestation by moths was quite high. In 1992, ca. 40% of the inflorescences were damaged in ES, while infestation was almost doubled (74%) in 1994. Considerable variation in pre-dispersal seed losses to insects over consecutive flowering/fruiting seasons has been found in other studies (e.g. De Steven 1983; Auld 1986; Andersen 1989). Some variation is usually attributed to differences in plant fecundity, although most remains unexplained because the dynamics of the insect population is not

studied. Substantial intraspecific variation in insect infestation may also have a large genetic component, as has been found by Larsson and Strong (1992) in *Salix viminalis* which is attacked by a gall midge.

The damage that the *Bruchophagus* wasps caused to the seeds of *E. dendroides* was quite important in some individuals. representing up to 93% of the seed crop. Seed predation by wasps was also greatly variable within the two populations, but in contrast to moth infestation, wasps were found to kill similar proportions of the seed crops in both areas. The levels of predation could not be attributed to plant size or number of fruits produced in any of the 3 years and no consistency among individuals across time was evidenced. i.e. a given plant could be highly damaged by wasps one year and suffer little predation the next season. This results contrast with others where fruit crop size does explain some of the variation in seed predation by insects (e.g. Roitberg et al. 1982; Jordano 1987: Traveset 1993). Predation intensity was much greater in 1992 than in the 2 following years, which was probably related to changes in the wasp population density. Insect population densities are known to vary strongly between seasons and may cause great variation in a given plant-insect interaction (e.g. Heithaus et al. 1982; Keeley et al. 1986; Randall 1986).

At the time of oviposition, *Bruchophagus* did not seem to discriminate between plants with different levels of infestation by moths. Therefore, the effect of these two insects on the plant reproductive losses appeared to be additive rather than counteracting one another in any way.

Of the seeds produced over the 3 years, between 20 and 34%. on average. were aborted. Considerable variation was observed at a spatial scale. some plants aborting all seeds and others aborting none. The consistency observed among individuals in seed abortion rates across years suggests that this reproductive loss is due to some factor(s) "intrinsic" to the plant rather than to something external such as weather conditions. Drought. for instance, has been found to influence the number of aborted seeds in several plant species (e.g. Lee and Bazzaz 1986; Jordano 1989), but this is less likely to explain variation among individuals growing in close proximity. The proportion of seeds aborted was similar between the two populations and was not related to plant size or fecundity. The main cause of seed abortion has been attributed to a limitation in resource availability (Stephenson 1981, but see Wiens et al. 1987), although it may also depend on paternity (e.g. Bookman 1984) or genetic deficiencies (Wiens et al. 1987).

After all the losses of reproductive potential outlined above, a rather low fraction of seeds per individual remain viable and is that which contributes to the next generation after being dispersed. The viable seed crop represented from 0 to 98% of the seeds produced and, on average, it never exceeded 40%. Even though the more fecund plants in the CG area produced a greater absolute number of viable seeds than plants in ES, the proportion of seeds that were viable did not differ significantly between the two populations in 1992 or in 1993. In 1994, however. seed predation was lower in CG and the relative number of viable seeds increased significantly in this area.

Seed viability was not associated with plant size or fecundity. and within a population, a larger plant did not necessarily produce more viable seeds. This has also been found in other systems (e.g. Traveset 1994) and is due to the great variability in reproductive losses during the pre-dispersal phase. Mainly because of the lack of consistency through time in seed predation by wasps, seed viability within a plant also varied greatly among years.

Cumulative effects of the reproductive losses

The four factors identified as reducing the potential number of seeds were of two types: (1) intrinsic to the plant (lack of ovaries/ovary abortion, and seed abortion), and (2) extrinsic to it (cyathia infestation by moths and seed predation by wasps). The cumulative fecundity reduction due to all of these factors was quite high during the 3 study years (87%–93%) in ES and during 1994 (64%) in CG.

Moth infestation was the most important loss in ES, followed by lack of ovaries/ovary abortion, seed damage by wasps and seed abortion. In contrast, moth infestation was negligible in CG whereas lack of ovary/ovary abortion represented the main loss of reproductive potential in this area. at least in 1994. Seed predation by wasps in CG was greater than seed abortion in 1992 and 1993. though these losses were similar in 1994. No correlations were found between losses due to moths and losses due to wasps. so these two species of insect do not appear to exert correlated selective pressures on plant traits such as those found in other studies (e.g. Evans et al. 1989).

The factor that showed the greatest variation among plants in pre-dispersal losses also varied between the two populations: in ES, the factor with the highest value of CV was seed abortion in 1992 and lack of ovaries/ovary abortion in 1993 and 1994, whereas in CG it was the plant interaction with the moth.

As found in other systems (Podoler and Rogers 1975; Heithaus et al. 1982; Jordano 1989; Traveset 1994). the key factor analyses show that the influence of a factor on among-plant variation in total reproductive loss may not be related to the magnitude of the pre-dispersal loss caused by that factor. Seed abortion accounted for the greatest among-plant variation in total loss of reproductive potential in all 3 years. although it caused a low reproductive loss (< 20%) relative to the other factors. Variation in time in such contributions were also observed in this study. so in 1994 infestation of cyathia by moths in the ES population had an important negative effect on reproductive

success and, at the same time, contributed greatly to the variation in total losses.

In summary, the insect-plant interactions in this system appear to vary spatially and temporally in their importance, both from an ecological and evolutionary viewpoint. Insect herbivores greatly reduce the average reproductive potential of *E. dendroides* but in most years contribute little to the variation among plants in total reproductive success. The lack of consistency in space and time, together with the lack of association between reproductive losses due to the insects and plant traits related to size and fecundity, suggest that if these insects exert a selective pressure on the plant promoting an adaptive change, this pressure is rather weak.

References

Alcover JA, Ballesteros E, Fornos JJ (1993) Història Natural de l'Arxipelag de Cabrera. Ed. Moll-CSIC, Palma de Mallorca

Andersen AA (1989) Pre-dispersal seed losses to insects in species of *Leptospermum* (Myrtaceae). Aust J Ecol 14: 13–18

Auld TD (1986) Variation in predispersal seed predation in several Australian *Acacia* spp. Oikos 47: 319–326

Bawa KS, Webb CJ (1984) Flower, fruit and seed abortion in tropical forest trees: implications for the evolution of paternal and maternal reproductive patterns. Am J Bot 71: 736–751

Bolós O (1958) Grupos corológicos de la flora balear. Publ Inst Biol Apl 27: 49–71

Bookman SS (1984) Evidence for selective fruit production in *Asclepias*. Evolution 38: 72–86

Breedlove DE, Ehrlich PR (1972) Coevolution: patterns of legume predation by a lycaenid butterfly. Oecologia 10: 99–104

Charlesworth D (1989) Why do plants produce so many more ovules than seeds? Nature 338: 21–22

Crawley MJ (1989) The relative importance of vertebrate and invertebrate herbivores in plant population dynamics. In: Bernays EA (ed) Insect-plant interactions, vol I. CRC Press, Boca Ratón, pp 45–71

Crawley MJ (1992) Seed predators and plant population dynamics. In: Fenner M (ed) Seeds, the ecology of regeneration in plant communities. CAB International, Wallingford, pp 157–191

De Steven D (1981) Predispersal seed predation in a tropical shrub (*Mabea occidentalis*, Euphorbiaceae) Biotropica 13: 146–150

De Steven D (1983) Reproductive consequences of insect seed predation in *Hamamelis virginiana* Ecology 64: 89–98

Ehrlén J (1991) Why do plants produce surplus flowers? A reserve-ovary model. Am Nat 138: 918–933

Evans EW, Smith CC, Gendron RP (1989) Timing of reproduction in a prairie legume: seasonal impacts of insects consuming flowers and seeds. Oecologia 78: 220–230

Green TW, Palmbald IG (1975) Effects of insect seed predators on *Astragalus cibarius* and *Astragalus utahensis* (Leguminosae). Ecology 56: 1435–1440

Hails RS, Crawley MJ (1991) The population dynamics of an alien insect: *Andricus quercuscalicis* (Hymenoptera: Cynipidae). J Anim Ecol 60: 545–562

Harper JL (1977) Population biology of plants. Academic Press, London

Harrison S (1987) Treefall gaps versus forest understory as environments for a defoliating moth on a tropical forest shrub. Oecologia 72: 65–68

Heithaus ER, Stashko E, Anderson PK (1982) Cumulative effects of plant-animal interactions on seed production by *Bauhinia ungulata*, a neotropical legume. Ecology 63: 1294–1302

Janzen DH (1971) Seed predation by animals. Annu Rev Ecol Syst 2: 465–492

Jordano P (1987) Avian fruit removal: effects of fruit variation, crop size, and insect damage. Ecology 68: 1711–1723

Jordano P (1989) Pre-dispersal biology of *Pistacia lentiscus* (Anacardiaceae): cumulative effects on seed removal by birds. Oikos 55: 375–386

Keeley JE, Keeley SC, Ikeda DA (1986) Seed predation by *Yucca* moths on semelparous, iteroparous and vegetatively reproducing subspecies of *Yucca whipplei* (Agavaceae). Am Midl Nat 115: 1–9

Krusi BO, Debusshe M (1988) The fate of flowers and fruits of *Cornus sanguinea* L. in three contrasting habitats. Oecologia 74: 592–599

Larsson S, Strong DR (1992) Oviposition choice and larval survival of *Dasineura marginemtorquens* (Diptera: Cecidomyiidae) on resistant and susceptible *Salix viminalis*. Ecol Entomol 17: 227–232

Lee TD, Bazzaz FA (1986) Maternal regulation of fecundity: nonrandom ovule abortion in *Cassia fasciculata* Michx. Oecologia 68: 459–465

Louda SM (1982a) Distribution ecology: variation in plant recruitment over a gradient in relation to insect seed predation. Ecol Monogr 52: 25–41

Louda SM (1982b) Limitation of the recruitment of the shrub *Haplopappus squarrosus* (Asteraceae) by flower- and seed-feeding insects. J Ecol 70: 43–53

Moore LR (1978) Seed predation in the legume *Crotalaria*. I. Intensity and variability of seed predation in native and introduced populations of *C. pallida* Ait. Oecologia 34: 185–202

Podoler H, Rogers D (1975) A new method for the identification of key factors from life-table data. J Anim Ecol 44: 85–114

Randall MGM (1986) The predation of predispersed *Juncus squarrosus* seeds by *Coleophora alticolella* (Lepidoptera) larvae over a range of altitudes in northern England. Oecologia 69: 460–465

Roitberg BD, Lenteren JC, Alphen JJM, Galis F, Prokopy RJ (1982) Foraging behaviour of *Rhagoletis pomonella*, a parasite of hawthorn (*Crataegus viridis*), in nature. J Anim Ecol 51: 307–325

SAS Institute Inc (1987) SAS/STAT guide for personal computers, version 6 Edn. SAS Institute, Cary, NC

Scott JK (1982) The impact of destructive insects on reproduction in six species of *Banksia* L. (Proteaceae). Aust J Zool 30: 901–921

Stephenson AG (1981) Flower and fruit abortion: proximate causes and ultimate functions. Annu Rev Ecol Syst 12: 253–279

Sutherland S (1986) Patterns of fruit-set: what controls fruit-flower ratios in plants? Evolution 40: 117–128

Thompson JN (1985) Postdispersal seed predation in *Lomatium* spp. (Umbelliferae): variation among individuals and species. Ecology 66: 1608–1616

Traveset A (1993) Weak interactions between avian and insect frugivores: the case of *Pistacia terebinthus* L. (Anacardiaceae). Vegetatio 107/108: 191–203

Traveset A (1994) Cumulative effects on the reproductive output of *Pistacia terebinthus* L. (Anacardiaceae). Oikos 71: 152–162

White TCR (1984) The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia 63: 90–105

Wiens D, Calvin CL, Wilson CA, Davern CI, Frank D, Seavey SR (1987) Reproductive success, spontaneous embryo abortion, and genetic load in flowering plants. Oecologia 71: 501–509